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Termite Foraging on Plants of a Brazilian Savanna: the Effects of Tree Height

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Abstract

Termites play an important role as ecosystem engineers in many tropical environments, acting as herbivore-detritivore organisms and strongly influencing vegetation structure and composition by modifying soil properties, providing nutrients by recycling the organic matter, and direct feeding on plants, notably in the Cerrado (Savanna) of Brazil. To evaluate the intensity of termite foraging on Cerrado plants, we recorded plants higher than 25 cm, which exhibited termite activity along nine transects (2 x 50m), at the Estação Ecológica de Pirapitinga (EEP), in the State of Minas Gerais, Brazil. We recorded the height, basal area, and identified the species of each plant. Simultaneously, we used cellulose baits disposed at each 10 m along six transects of 100 m to sample termites in this area, which was protected from fire for at least 40 years. Twelve species of termites were recorded. Termite foraging on Cerrado plant species varied considerably and it was influenced by several factors including plant height and host species. Taller plants presented more termites than smaller plants, probably due to the amount of available resources (for nesting and feeding) for the termites.

Introduction

Termites are eusocial insects presenting high richness and abundance in tropical regions (Wood & Sands, 1978; Collins, 1983; Eggleton, 2000). They play an important role in nutrient and carbon flows (Lawton et al., 1996; Bignell et al., 1997; Tayasu et al., 1997), and strongly affect the soil structure due to their positive impact on porosity, aeration, infiltration, and nutrient storage (Lee & Foster, 1991; Mando et al., 1996). Termites also act as decomposers of organic matter (Bignell & Eggleton, 2000), and their activities may strongly affect the distribution of plant and animal species because: i) termite nests concentrate nutrients; old nests can be important for the population dynamics of some species of plants that benefit from a more fertile soil for seed germination and seedling development (Ackerman et al., 2007; Traoré et al., 2008; Beaudrot et al., 2011); ii) termite nests serve as shelter

and nesting sites for many species of animals, including other termite species (Marins et al., 2016); iii) many animals depend on termites for nutrition (Redford & Dorea, 1984); and iv) several symbiont organisms occur associated only with certain termite species (Spain & McIvor, 1988; Whitford, 1991; Lavelle, 1997; Cristaldo et al., 2012).

Termites feed primarily on cellulose and substances derived from the degradation of the cellulose and lignin, found in a wide variety of dead or live plant tissues, complete or partially decomposed material, such as leaves, seeds, wood, roots, litter, humus and feces (reviewed in Lima & Costa-Leonardo, 2007). Some species, however, may specialize on a certain subset of resources and may attack live plant parts (see Sands, 1969; Lee & Wood, 1971). They feed on roots or dig galleries in the trunk, occasionally causing the death of the plant (Rao et al., 2000; Sileshi et al., 2005). Frequently, an attack starts on the dead tissues and later expands to the



live plant parts (Costa Lima, 1938). Attacks to plant stems may also be related to damage inflicted by fungi (Wood et al., 1980). Some studies have also established links between termite attacks on plants and low soil fertility (Wardell, 1987) or water stress suffered by plants (Rao et al., 2000; Van den Berg & Rieckert, 2003).

The dynamics, ontogeny and architecture of the aerial plant parts play a crucial role on the abundance and structure of their associated insect communities (Lawton, 1983; Strong et al., 1984; Fonseca et al., 2006). Generally, larger trees support higher richness and abundance of insects than smaller trees (Price, 1997; Basset, 2001; Barrios, 2003). Although termite preferences for Cerrado species varies widely, plant morphological traits such as size, height and trunk circumference are thought to play important roles on the insect activities (Gonçalves et al., 2005; Lima-Ribeiro et al., 2006; Araújo et al., 2010). Specifically for *Constrictotermes cyphergaster* (Silvestri), the diameter and inclination of the stem, branching density, tree height, and soil type affect the colonization, establishment, nest shape and colony size in the Cerrado (Cunha, 2000; Lima-Ribeiro et al., 2006).

Here, we evaluated the effects of plant species and plant dimensions (measured as height and basal area) on the intensity of termite foraging and provided the first survey of termite species in the Estação Ecológica de Pirapitinga (EEP). We tested the hypothesis that there is a positive relationship between termite intensity of foraging and the dimension of the structures of trees in the EEP. Such hypothesis was based on the findings by Gonçalves et al. (2005), Lima-Ribeiro et al. (2006), Araújo et al. (2010) and Leite et al. (2011) that have shown that larger trees may present higher quantity and availability of resources for their associated termite species.

Materials and Methods

Study Area

This study was carried out in an area of Cerrado vegetation belonging to the Estação Ecológica de Pirapitinga (EEP). The EEP is an island formed by the creation of the dam of Três Marias in the São Francisco river in 1965. The island has 1090 ha in area and it is located between 18°20'S - 18°23'S and 45°17'W - 45°20'W, at an altitude of 570 to 630 m above sea level (Azevedo et al., 1987), in the municipality of Morada Nova de Minas, in the State of Minas Gerais, southeastern Brazil. In some years, during the dry season, the EEP may form a peninsula and be reconnected to the surrounding vegetation.

The vegetation in the station can be assigned to three main Cerrado physiognomies: campo sujo, Cerrado *sensu stricto*, and cerradão (Gonçalves-Alvim & Fernandes, 2001). This study has been conducted in an area of Cerrado *sensu stricto*. Such a physiognomy is characterized in the station by low stature trees (3-6 m height), that present thick bark and sclerophyllous leaves (Oliveira & Marquis, 2002).

Climate is tropical, fitting to Aw type in Köppen-Geiger's classification, bearing a long dry season (up to four months) between May and September (Gonçalves-Alvim & Fernandes, 2001) and a rainy season between October and April. Average monthly temperature varies between 20.9 and 25.1°C, and the average annual rainfall is 1.222 mm. Heavily clayish, dystrophic dark red, oxysols dominate the gently undulated topography. Some areas, however, present dystrophic to moderate cambisols in undulated to strongly undulated topography (Azevedo et al., 1987).

Termite sampling using baits

To survey termite fauna in EEP, termite sampling followed a method modified from La Fage et al. (1973). Six 100 m long transects were randomly allocated in the field, within which unscented toilet paper rolls (10 cm wide × 30 m long, forming a 10 cm Ø roll) were regularly distributed at each 10 m. Soil surface was brushed off before receiving the paper rolls, assuring full contact of the bait to the soil. Baits were covered by a black polyethylene bag (20 × 33 cm) and held in place by an inverted "U" wire inserted through the bait until 15 cm deep in the soil. Empty and washed PET (polyethylene terephthalate) bottles, 2 L in volume, cut in halves perpendicular to the main axis were placed covering the bait for improved protection. Rolls thereby arranged had their bottom surface in full contact with the soil.

In addition to termite sampling using baits, as mentioned above, samples in the interior of the trunk of five plant individuals subjected to strong attack by termites were performed to complement the species sampling.

Sampling was carried out from May to August 2005 (what corresponds to the dry period in the station). Termites were collected 95 days after the beginning of the experiment. In a pilot assay with another set of baits, this period corresponded to the time needed to detect the total (100%) consumption of the first bait by termites. In case the bait was totally consumed, termite attack was identified by indirect evidence, such as dead corpses of termites. Baits were taken to the laboratory to quantify termites by direct count of individuals, preservation in 70% ethanol, and identification to species.

Plant species survey

Plant sampling was carried out from May to September 2005. To evaluate the effect of total tree height, basal area, and plant species on intensity of attack by termites, nine transects (2 m wide × 50 m long) were randomly marked in the field. Within each transect, the above parameters were measured in every plant above 25 cm high.

Assessment of termite foraging on living plants

Termite foraging was categorized into four levels considering the intensity of attack (ia0, ia1, ia2, and ia3; see Table 1) through the colonization process and injuries inflicted

to the plant (modified from Anonymous, 1989). Every plant was visually inspected to record presence/absence of termites or their signs (galleries or nests). Stems having termites and bearing injuries clearly attributable to them were evaluated at several positions on the plant in order to record whether the injury was deeper than the bark thickness (Fig 1). An additional survey of termites in heavily attacked plants was performed aiming to confirm termite attacks.

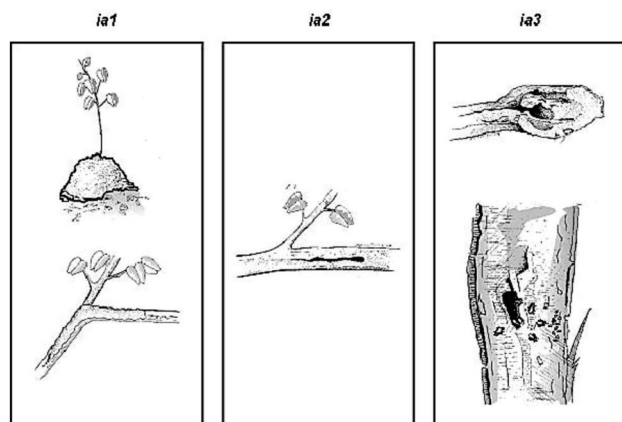


Fig 1. Schematic illustration of the categories of intensity of attack (*ia*) by termites on plants of Cerrado in the Estação Ecológica de Pirapitinga - Minas Gerais. *ia1* - Presence of termites with no attack - termite nests constructed around a plant stem, but without evidence of attack or gallery construction. *ia2* - Attack limited to the bark - gallery construction on a branch, displaying the damage to the bark. *ia3* - Severe attack - transversal section of one trunk severely damaged in its internal structure and still with presence of termites.

Statistical Analyses

In order to know whether sampling effort was enough to quantify plant species, we calculated the estimators *Chao1* (based on abundance) and *Chao2* (based on incidence) using EstimateS Version 7.5.0 (Colwell, 2005). Plant basal area was estimated using the general equation for the area of a circle [$A = (\pi D^2)/4$; where A is the basal area, π is the value of the constant Pi, and D is the stem diameter at the point where the plant touches the soil surface].

To guarantee accurate estimation of effects within plant species, statistical analysis has been conducted using a sub-set

of the nine most abundant plant species, among the 51 recorded along the transects. Each of these nine plant species presented a minimum of 20 individuals, and represented as a whole, 60.33 % of all plant individuals recorded. To check whether termite attack intensity (*y*-var) correlated with plant traits (*x*-vars: height, basal area and plant identity), we performed multiple regressions under the Generalized Linear Modelling (R Development Core Team, 2006). The full model, therefore, was: $ia \sim species + height + basalArea + species:height + species:basalArea + species:height:basalArea$; where *ia* = intensity of attack, *species* = plant species identity, *height* = plant height, *basalArea* = area of plant stem where it touches the soil surface. Model simplification was achieved contrasting a complex model with an alternative simpler one built by removing variables and interactions, and merging levels within categorical variables, as long as such a simplification did not cause significant ($P < 0.05$) changes in the model. Every time a simplification was accepted, the resulting model was then contrasted again with an even simpler model and hence consecutively until a minimal adequate model was achieved. This minimal model was composed only by significant terms. Residuals were inspected to check for the suitability of the model and error distribution.

The categorical variable *species*, initially composed of nine levels (each of the nine most abundant plant species included in the analysis), was grouped following recommendations by Crawley (2007). After calculating parameter values for each of the species, we ordered these parameters from smaller to larger, creating a simpler model in which the variable *species* entered with its levels merged in groups according to the significance of their parameters. To do such a merging, the levels presenting adjacent parameter values were amalgamated in a single level and the resulting model was contrasted with the previous and more complex one. This was done successively until merging caused significant changes ($P < 0.05$) in the simpler model. At this point, a species group was defined. Merging proceeded, creating a second grouping of plant species merging the subsequent levels according to proximity of their parameter values and contrasting the resulting models as before. This proceeded until no further grouping was possible without causing significant changes.

Table 1. Categories of attack intensity by termites on the Cerrado plants in the Estação Ecológica de Pirapitinga - Minas Gerais. Adapted from Anonymous (1989).

Intensity of attack (<i>ia</i>)	Description
<i>ia0</i> : Absence of termites	Plants do not present evidences of termites, without any constructed structures and/or damaged parts attributable to the attack of termites.
<i>ia1</i> : Presence of termites without attack	Plants with presence of termites and/or active structures of termites, but without damaged parts attributable to their attack.
<i>ia2</i> : Attack limited to the bark.	Plants with termites and superficial damage limited to the bark attributable to the attack of termites.
<i>ia3</i> : Severe attack	Plants with termites and attack visibly crossing the bark and the central part of trunk (sapwood/heartwood). They could present trunk and branches very damaged or deceased, and leaf withering. Plants can still present new shoots coming out of the root.

Results

The termite survey revealed the presence of 12 termite species in the EEP, distributed in two families (Table 2). Seven species were recorded on the toilet paper baits while eight species were recorded in the tree trunks. Four termite species were only recorded on the baits while five species were only found by manually collection inside tree trunk samples of five plants arbitrarily selected and strongly attacked (Table 2). *Nasutitermes* aff. *coxipoensis* was the most abundant species collected on the toilet paper baits, composing more than half of the individuals collected, while *Heterotermes sulcatus* was the second most abundant species, with 35% of the individuals collected (Table 2).

The distance between the observed accumulation curve for plant species and the curves for estimators *Chao1* and *Chao2* were, respectively, 7.2 and 3.6 (Fig 2). Such values indicate that 88 to 93% of the local arboreal and shrubby plant species were effectively recorded by the sampling procedure and that, as shown in Fig 2, a considerable effort would be needed in order to improve this sampling.

A total of 713 plant individuals belonging to 51 species and 28 families were surveyed (Table 3). Among plant individuals, 49% did not show signs of termite presence

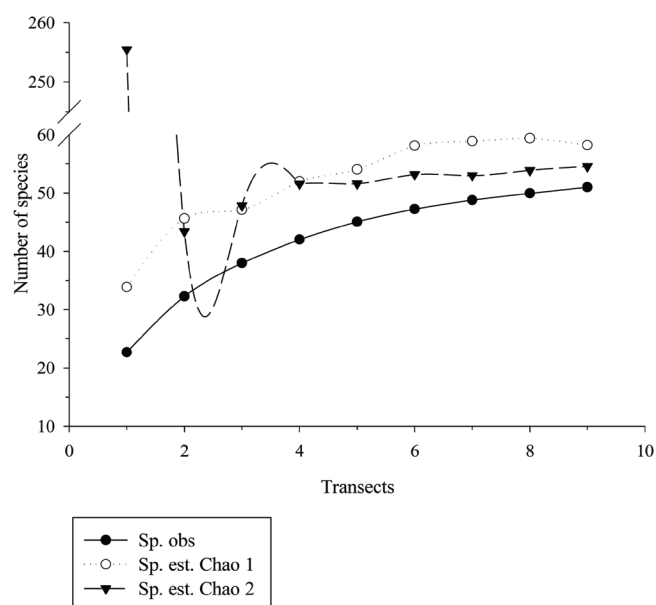


Fig 2. Plant species accumulation according to *Chao1* and *Chao2* estimators and observed accumulation of species of plants in the Cerrado of the Estação Ecológica de Pirapitinga - Minas Gerais (see text for details). Axis Y (species number) was interrupted in interval 60 - 245 for better visualization of the figure.

Table 2. Termite species found in the Cerrado of the Estação Ecológica de Pirapitinga and their relative abundance and frequency in baits and in tree trunks. Feeding groups (according to Constantino 2015): Xyl = xylophagous, wood-feeder; Lit = litter-feeder; Int = intermediate (species that feeds on wood and litter); Spe* = specialized feeder.

Family/Species	Feeding group	Collection		Number of Individuals (%)	Percent of records in baits
		Baits	Tree trunks		
Rhinotermitidae					
<i>Heterotermes sulcatus</i> Mathews	3. Xyl	X		8,437 (34.7%)	19.0%
Termitidae					
Subfamily Nasutitermitinae					
<i>Constrictotermes cyphergaster</i> (Silvestri)	Spe*	X		42 (0.2%)	1.7%
<i>Nasutitermes</i> aff. <i>coxipoensis</i> (Holmgren)	Lit	X	X	13,363 (54.9%)	43.1%
<i>Nasutitermes kemneri</i> Snyder & Emerson	Xyl		X	-	
<i>Parvitermes bacchanalis</i> Mathews	Lit	X		768 (3.2%)	6.9%
<i>Velocitermes</i> sp.	Lit	X	X	1,049 (4.3%)	15.5%
<i>Velocitermes</i> cf. <i>paucipilis</i> Mathews	Lit		X	-	
Subfamily Syntermitinae					
<i>Cornitermes silvestrii</i> Emerson	Lit	X		526 (2.2%)	12.1%
<i>Rhynchotermes nasutissimus</i> (Silvestri)	Lit		X	-	
<i>Silvestritermes euamignathus</i> (Silvestri)	Int	X	X	143 (0.6%)	1.7%
Subfamily Termitinae					
<i>Microcerotermes strunckii</i> (Sørensen)	Xyl		X	-	
<i>Termes nigrinus</i> (Silvestri)	Int		X		
Total		7	8	24,328 (100%)	100%

* According to our observations, *C. cyphergaster* forages on trees, scraping the surface and feeding mostly on tree barks, soft dead plant tissue, and lichens. It does not feed on wood and is not a litter-feeder.

Table 3. Records of the plant species, with their respective abundance (AB), average height and basal area (\pm SE) in the Estação Ecológica de Pirapitinga - Minas Gerais.

Family	Species	AB	Height (m)	Basal area (cm ²)
Annonaceae	<i>Annona</i> sp.	36 (5.0%)	2.65 \pm 0.30	29.03 \pm 7.57
	<i>Duguetia furfuraceae</i>	15 (2.1%)	1.43 \pm 0.12	4.87 \pm 1.33
	<i>Rollinia</i> sp.	8 (1.1%)	2.47 \pm 0.25	6.77 \pm 1.35
	<i>Xylopia aromatica</i>	28 (3.9%)	3.43 \pm 0.57	31.82 \pm 9.29
Apocynaceae	<i>Aspidosperma tomentosum</i>	5 (0.7%)	2.35 \pm 1.05	41.48 \pm 35.47
Araliaceae	<i>Schefflera macrocarpa</i>	11 (1.5%)	2.46 \pm 0.53	27.23 \pm 6.35
Asteraceae	<i>Piptocarpha cf. rotundifolia</i>	1 (0.1%)	2.35	6.16
	<i>Piptocarpha rotundifolia</i>	7 (1.0%)	3.73 \pm 0.69	25.74 \pm 7.71
Bignoniaceae	<i>Tabebuia ochracea</i>	3 (0.4%)	3.85 \pm 2.98	11.58 \pm 1.66
Bombacaceae	<i>Eriotheca gracilipes</i>	14 (2.0%)	3.78 \pm 0.86	40.83 \pm 16.67
Burseraceae	<i>Protium cf. brasiliense</i>	2 (0.3%)	1.70 \pm 0.41	2.32 \pm 0.55
Clusiaceae	<i>Kielmeyera coriacea</i>	9 (1.3%)	3.35 \pm 0.86	84.57 \pm 56.10
Dilleniaceae	<i>Davilla rugosa</i>	6 (0.8%)	1.17 \pm 0.18	4.22 \pm 1.82
Ebenaceae	<i>Diospyros</i> sp.	8 (1.1%)	5.69 \pm 0.80	60.50 \pm 22.14
Erythroxylaceae	<i>Erythroxylum tortuosum</i>	1 (0.1%)	2.30	27.34
Fabaceae	<i>Acosmium dasycarpum</i>	9 (1.3%)	5.52 \pm 1.75	91.20 \pm 40.82
	<i>Bauhinia brevipes</i>	31 (4.3%)	2.32 \pm 0.27	7.00 \pm 0.67
	<i>Dimorphandra mollis</i>	19 (2.7%)	2.11 \pm 0.55	11.32 \pm 4.83
	<i>Enterolobium gummiferum</i>	1 (0.1%)	2.67	8.77
	<i>Hymenaea stigonocarpa</i>	5 (0.7%)	4.66 \pm 1.37	60.39 \pm 24.65
	<i>Pterodon emarginatus</i>	20 (2.8%)	5.23 \pm 0.81	98.47 \pm 43.13
	<i>Stryphnodendron adstringens</i>	8 (1.1%)	3.51 \pm 0.96	41.30 \pm 14.91
Flacourtiaceae	<i>Casearia cf. arborea</i>	18 (2.5%)	1.70 \pm 0.24	6.81 \pm 1.47
Loganiaceae	<i>Strychnos</i> sp.	2 (0.3%)	6.88 \pm 5.13	13.78 \pm 12.01
Malpighiaceae	<i>Banisteriopsis</i> sp.	5 (0.7%)	3.13 \pm 1.41	16.31 \pm 9.51
	<i>Byrsonima cf. sericea</i>	7 (1.0%)	1.82 \pm 0.32	14.69 \pm 6.04
	<i>Byrsonima</i> sp.	1 (0.1%)	3.50	24.37
	<i>Heteropteris</i> sp.	5 (0.7%)	4.59 \pm 1.05	34.87 \pm 13.50
	<i>Tetrapteris ramiflora</i>	1 (0.1%)	8.00	111.91
Melastomataceae	<i>Miconia albicans</i>	209 (29.3%)	1.92 \pm 0.06	7.77 \pm 0.87
	<i>Miconia</i> sp.	2 (0.3%)	1.88 \pm 0.13	2.58 \pm 0.57
Monimiaceae	<i>Siparuna guianensis</i>	28 (3.9%)	2.45 \pm 0.24	4.50 \pm 1.25
Moraceae	<i>Ficus</i> sp.	5 (0.7%)	1.31 \pm 0.20	4.56 \pm 1.96
Nyctaginaceae	<i>Neea theifera</i>	2 (0.3%)	1.84 \pm 0.17	13.02 \pm 5.84
Ochnaceae	<i>Ouratea cf. castaneifolia</i>	1 (0.1%)	0.75	1.99
	<i>Ouratea cf. hexasperma</i>	1 (0.1%)	3.40	13.45
	<i>Ouratea semiserrata</i>	13 (1.8%)	2.17 \pm 0.39	16.47 \pm 3.60
Proteaceae	<i>Roupala montana</i>	9 (1.3%)	2.68 \pm 0.50	39.01 \pm 10.58
Rubiaceae	<i>Alibertia edulis</i>	1 (0.1%)	2.50	0.97
	<i>Coussarea</i> sp.	21 (2.9%)	2.91 \pm 0.49	10.76 \pm 3.59
	<i>Guettarda</i> sp.	4 (0.6%)	6.13 \pm 1.21	90.85 \pm 39.24
	<i>Tocoyena cf. formosa</i>	11 (1.5%)	2.23 \pm 0.60	14.15 \pm 4.19
Sapindaceae	<i>Matayba mollis</i>	16 (2.2%)	2.87 \pm 0.47	18.92 \pm 7.82
	<i>Serjania</i> sp.	4 (0.6%)	3.46 \pm 1.45	47.29 \pm 24.54
Sapotaceae	<i>Pouteria ramiflora</i>	14 (2.0%)	2.22 \pm 0.36	16.55 \pm 4.19
	<i>Pouteria torta</i>	4 (0.6%)	4.69 \pm 1.88	109.07 \pm 53.02
Vochysiaceae	<i>Qualea multiflora</i>	31 (4.3%)	2.52 \pm 0.35	34.68 \pm 9.31
	<i>Qualea parviflora</i>	6 (0.8%)	2.99 \pm 0.45	21.58 \pm 4.40
	<i>Qualea grandiflora</i>	26 (3.6%)	2.85 \pm 0.47	58.67 \pm 19.30
	<i>Qualea</i> sp1.	1 (0.1%)	3.00	55.88
	<i>Qualea</i> sp2.	18 (2.5%)	2.28 \pm 0.26	22.59 \pm 6.23
28 families	51 species	713 (100%)		

or attack ($ia = 0$), 22% presented termites but did not show signs of attack ($ia = 1$), 16% presented signs of attack to the bark ($ia = 2$), and 13% presented severe attack ($ia = 3$) (Fig 3). Only nine plant species were represented by 20 or more individuals (Table 3). These nine plant species were selected to perform the analyses and summed 430 individuals or 60.33% of the total of plant individuals sampled. Among these, 57.91% did not show any sign of termite presence or their attack. The proportion of attacked plants decreased as attack intensity increased (Table 4).

The intensity of termite attack on these plants may be explained by plant height and identity. Three groups of

plants were distinguished according to the pattern of response of termite attack to plant height. These groups resulted from merging levels (plant species) within categorical variable *species*, as described in the Material and Methods section. Group 1 comprised *Annona* sp., *Pterodon emarginatus*, *Qualea grandiflora* and *Q. multiflora*. Group 2 was composed of solely *Bauhinia brevipes*, and Group 3 was composed of *Xylopia aromatica*, *Miconia albicans*, *Siparuna guianensis* and *Coussarea* sp. (Table 5, Fig 4). Termite attack intensity increased as plant height increased in groups 1 and 3 while a negative trend was observed on group 2 solely formed by the shrub *Bauhinia brevipes*.

Table 4. Abundance and percentage of plant individuals found in the categories of termite attack intensity in the nine vegetal species represented by 20 or more individuals in the sampling in the Estação Ecológica de Pirapitinga - Minas Gerais. Bold indicates the most observed levels of attack intensity in each group.

Species (Family)	<i>ia0</i>	<i>ia1</i>	<i>ia2</i>	<i>ia3</i>	Total
<i>Annona</i> sp. (Annonaceae)	10 (2.3%)	9 (2.1%)	14 (3.3%)	3 (0.7%)	36 (8.4%)
<i>Pterodon emarginatus</i> (Fabaceae)	3 (0.7%)	7 (1.6%)	8 (1.9%)	2 (0.5%)	20 (4.6%)
<i>Qualea grandiflora</i> (Vochysiaceae)	5 (1.2%)	7 (1.6%)	7 (1.6%)	7 (1.6%)	26 (6.0%)
<i>Qualea multiflora</i> (Vochysiaceae)	3 (0.7%)	11 (2.6%)	12 (2.8%)	5 (1.2%)	31 (7.2%)
<i>Bauhinia brevipes</i> (Fabaceae)	1 (0.2%)	2 (0.5%)	4 (0.9%)	24 (5.6%)	31 (7.2%)
<i>Xylopia aromatica</i> (Annonaceae)	15 (3.5%)	8 (1.9%)	3 (0.7%)	2 (0.5%)	28 (6.5%)
<i>Miconia albicans</i> (Melastomataceae)	179 (41.6%)	18 (4.2%)	11 (2.6%)	1 (0.2%)	209 (48.6%)
<i>Siparuna guianensis</i> (Monimiaceae)	23 (5.3%)	4 (0.9%)	0 (0.0%)	1 (0.2%)	28 (6.5%)
<i>Coussarea</i> sp. (Rubiaceae)	10 (2.3%)	9 (2.1%)	2 (0.5%)	0 (0.0%)	21 (4.9%)
Total	249 (57.9%)	75 (17.4%)	61 (14.2%)	45 (10.5%)	430 (100%)

Discussion

Termite Species

The ecological station where we conducted this study was protected from fire and human disturbance for at least 40 years, but according to our results, the recorded termite fauna

was similar to other Cerrado physiognomies (Constantino, 2005; Nunes et al., 2016), including areas where fire has occurred with some frequency (DeSouza et al., 2003).

Termites feed generally on lignified parts of live plants, although roots may represent an important route to invasion of the host plant (Lee & Wood, 1971; Waller & LaFage, 1987).

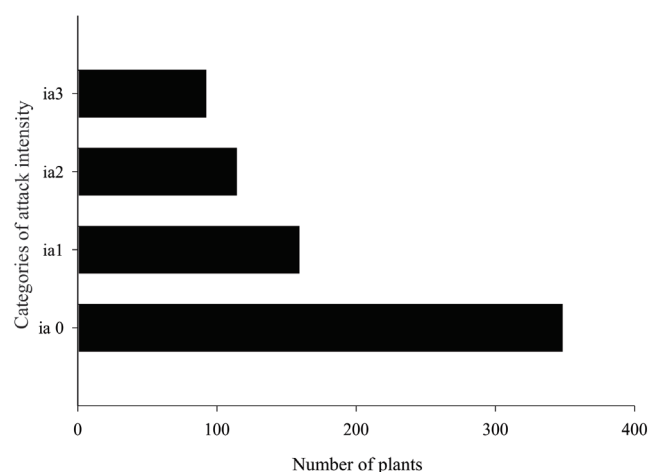


Fig 3. Number of individuals in each category of intensity of attack (*ia*) of termites in the vegetation of the Cerrado of the Estação Ecológica de Pirapitinga - Minas Gerais. *ia0*: Absence of termites; *ia1*: Presence of termites without attack; *ia2*: Attack limited to the bark; and *ia3*: Severe attack.

Table 5. Effect of height of the plant species on the intensity of attack by termites in the Cerrado of the Estação Ecológica de Pirapitinga - Minas Gerais. The adjusted minimum model was: $ia \sim species_group + tree_height + species_group:tree_height$ where species group contains three groups of species that responded differently in the presented intensity of attack: group 1 (*Annona* sp., *Pterodon emarginatus*, *Qualea grandiflora* and *Qualea multiflora*), group 2 (*Bauhinia brevipes*), and group 3 (*Xylopia aromatica*, *Miconia albicans*, *Siparuna guianensis* and *Coussarea* sp.). df = degrees of freedom.

Source of variation	df	Deviance	F	P
Species Group	2	231.46	238.312	<0.0001 (2.2e ⁻¹⁶)
Tree Height	1	19.20	38.529	<0.0001 (8.045e ⁻¹⁰)
Species Group: Tree Height	2	11.10	11.431	<0.0001 (1.462e ⁻⁰⁵)
Error	424	205.91		
Total	429	467.67		

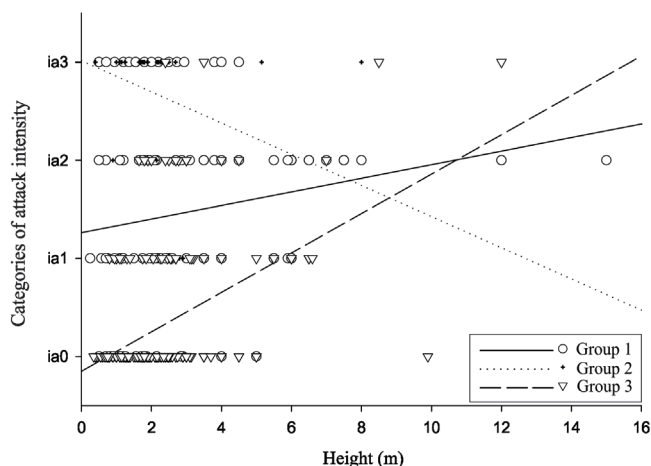


Fig 4. Effect of the size of plant species on the intensity of attack by termites in the Cerrado of the Estação Ecológica de Pirapitinga. The adjusted minimum model presents three distinct groups based on intensity of termite attack: Group 1 – continuous line (*Annona* sp., *Pterodon emarginatus*, *Qualea grandiflora* and *Qualea multiflora*); Group 2 dotted line (*Bauhinia brevipes*); and Group 3 hatched line (*Xylopia aromatic*, *Miconia albicans*, *Siparuna guianensis* and *Coussarea* sp.).

The xylophagy is maintained in most groups of termites, including many derived species from the subfamily Nasutitermitinae (Termitidae) and species of the genus *Heterotermes* (Rhinotermitidae) (Mathews, 1977; Engel & Krishna, 2004; Engel, 2011).

Many species of *Nasutitermes* build their nests on host trees and have been associated with wood damages (Thorne, 1980; Santos, 1982; Bandeira et al., 1998), but the most abundant species found in this study was *N. aff. coxipoensis*, which is a mound-building termite (Laffont et al., 2012). It presents a wide range of food resources, including dead wood from trunks of living trees, which may be deeply excavated by these insects (Laffont et al., 1998, 2012).

The genus *Heterotermes* comprises several termite species that have a status as pests, such as *H. tenuis* (Pizano & Fontes 1986; Haifig et al., 2008), *H. longiceps* (Pizano & Fontes, 1986; Calderon & Constantino, 2007) and *H. sulcatus* (Vasconcellos et al., 2002). This latter species has been considered one of the most important xylophagous species in Caatinga vegetation, where it feeds preferentially on dead wood (Mélo & Bandeira, 2007). In this latter environment, other important xylophagous species such as *Nasutitermes* and *Microcerotermes* are rare or missing (Mélo & Bandeira, 2004). In our study, *H. sulcatus* was the second most abundant termite species, therefore being responsible for a great amount of plant attack.

The additional survey in the interior of plant trunks revealed eight species, and four of which were solely found there: *Microcerotermes strunckii*, *Nasutitermes kemneri*, *Rhynchotermes nasutissimus*, and *Termes nigrinus*. Casual observation in the site also revealed that *Syntermes nanus* Constantino, a Syntermitinae, leave their subterranean nests to forage on grasses. These additional observations reinforced the relevance of the Nasutitermitinae-Syntermitinae group

in the Cerrado, as these groups were particularly sampled in our studies. Overall, many of the termite species may be associated to plant damage (Murcia et al., unpublished data), indicating the need for more detailed studies on termite-plant association in the several Cerrado physiognomies.

Termite-plant interactions

Plant height positively affected the intensity of termite attack in eight out of nine plant species, therefore corroborating the hypothesis that larger plants are more attacked than smaller ones. Such a hypothesis was also corroborated by other studies that show a positive relationship between herbivore species richness and size of the host plant (e.g., Lawton, 1983; Strong et al., 1984; Gonçalves et al., 2005). Termite feeding preferences for some plant species in field studies were recorded by Wood (1978), whereas Gontijo (1991) and Cunha (2000) provided some data on such relationships in the Brazilian Cerrado. Our results also show a variation in termite attack to plant species that can be summarized into two general patterns: (i) for most plants, the larger they are the more they are attacked and (ii) for a single plant species, *B. brevipes*, the opposite trend was observed.

Larger plants are more attacked by termites than smaller plants possibly because: (i) they offer more food to termites (Gonçalves et al., 2005), (ii) they present better possibilities for foraging activities (Jones & Gathorne-Hardy, 1995; Gonçalves et al., 2005), and/or (iii) they provide better opportunities to escape predators (Neves et al., 2014; Pequeno, 2017). Furthermore, larger plants may constitute a better resource for tree-nesting termites. Cunha (2000) showed that *C. cyphergaster* prefers to build its nest in trees with 71 to 286 cm² of basal area. Among the plants sampled here, only 20 individuals (*P. emarginatus*) presented such dimensions and, among these, 85% presented termites and 50% presented attack intensity of levels ia2 and ia3. Taller plants also bear larger bark surfaces, which in consequence present greater food resources for termites (Jones & Gathorne-Hardy, 1995). Similarly, larger plants tend to bear more complex architecture, presenting more ramifications (Gontijo, 1991) and more epiphytes. We suggest that both, ramifications and epiphytes, may increase the chance to accumulate dead organic matter in the form of 'suspended litter' which, at the end, represents more food to termites, as observed in other ecosystems (Gonçalves et al., 2005). A study by Roisin et al. (2006) showed that soil-feeder termites, for example, were absent from the canopy in a tropical rainforest because larger epiphytes were lacking.

Larger plants are more attacked than smaller plants due to larger supply of food and foraging sites, indicating that plant age is also an important variable to be discussed. It is expected that older plants presented larger trunks and stems, and more natural dead trunks, stems and roots, offering attractive resources to termites. On the other hand, this variable may be complicated to be measured in the field, because larger plants are not necessarily older.

It is likely that plant encounter by termites may occur simply by chance, without any relationship to plant nutritional quality (Nutting, 1969; Souto et al., 1999). In such cases, taller plants would be found more easily, simply because they are more conspicuous (Gonçalves et al., 2005; Araújo et al., 2010). Such a circumstance may define a random pattern for termite distribution on host plants. However, this pattern may not stay strictly in the random realm, because after finding the plant, termites may be subjected to other non-random factors (such as plant chemical traits), which may define whether or not termites would settle themselves on the plant found. The nutritional quality of the plants and their chemical defenses against the attack by insects could also exert a relevant role in the behavior of attack of termites and susceptibility of the plant. However, such studies on termites are scarce and need to be carried out at population, community, and ecosystem levels, before drawing any conclusion.

By exposing internal parts of the plant, higher intensity of attack may lead to easier contamination by pathogens (Sellschop, 1965). Interestingly, several termite species prefer plant tissues partially altered by fungi action, including termite species which are able to attack sound wood (Noirot & Noirot-Timotheé, 1969). In the present study, termite attack was observed to occur along with fungi on *B. brevipes* individuals, the only plant species where termite attack correlated negatively with plant size. We hypothesize that the concurrent action of termites and fungi may have promoted branch loss in this species, in such a way that attack could lead to smaller sizes. This would explain the observed negative correlation between termite attack and *B. brevipes* size.

Bauhinia brevipes is a shrub typical to Cerrado, growing up to three meters height, and presenting a rich fauna of herbivore insects, including many galling species (Fernandes, 1998; Fernandes et al., 2000; Cornelissen & Fernandes, 2001; Maia & Fernandes, 2005). Heavy activity of *Nasutitermes* spp. was observed in the damaged stems of *B. brevipes*. That is, *B. brevipes* individuals presenting higher attack intensities ($ia = 3$) were also the shortest individuals in the population, because their size was reduced by the loss of main stems caused by termite attack. This would, then, produce the observed negative relationship between termite attack intensity and *B. brevipes* size. The system termite - *B. brevipes* - galling herbivores may represent an interesting scenario, yet to be explored, where termite attack may induce the host plant to continually produce new shoots (new meristems) which are then attacked by leaf galling insects. This may represent another avenue for research in this tropical and dynamic ecosystem where termites may exert an important, yet not well known, role by manipulating the resources used by herbivores.

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Authors contribution

Experimental design (G.W.F., S.L.M.), sampling data (S.L.M., J.C.S.), species identification (R.C.), statistical analysis (S.L.M., J.C.S., O.D.), text review (G.W.F., S.L.M., J.C.S., O.D., R.C., I.H.). All authors discussed and revised the manuscript.

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